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Maractis rimicarivora, a new genus and species of sea anemone (Cnidaria: Anthozoa: Actiniaria: Actinostolidae) from an Atlantic hydrothermal vent

Daphne G. Fautin and Brian R. Barber

Division of Biological Sciences and KU Natural History Museum, University of Kansas, Lawrence, Kansas 66045, U.S.A.

Abstract.—*Maractis rimicarivora* is a new genus and new species of medium-sized sea anemone (Actiniaria) from the TAG (Trans-Atlantic Geotraverse) hydrothermal vent fields (26°08.3′N, 44°49.6′W; 3650 m). The genus, which belongs to family Actinostolidae, is distinguished by the following combination of features: six pairs of complete mesenteries, mesenteries not arrayed according to the *Actinostola* rule, all mesenteries gametogenic, tentacles not thickened at the base, and no tentacular mastigophores. The species is distinguished by long, longitudinally-furrowed tentacles, and a roughened column. Anemones of this species encircle black smokers at distances from 15 to 60 m. This is the second species to be reported from hydrothermal vents of the Atlantic. Four species have been reported from Pacific hydrothermal vents.

Five species of sea anemones have been documented from hydrothermal vents (Desbruyères & Segonzac 1997). *Cyananthea hydrothermala* Doumenc & Van-Praët, 1988, and *Marianactis bythios* Fautin & Hessler, 1989, were described from Pacific vents. Doumenc & Van-Praët (1988) also identified from Pacific vents *Actinostola callosa* (Verrill, 1882) and *Chondrophellia coronata* (Verrill, 1883), species described from trawled specimens before the existence of hydrothermal vents was known. The only sea anemone thus far reported from Atlantic vents is *Parasicyonis ingolfi* Carlgren, 1942 (Segonzac 1992), another species described from trawled specimens. Certainly three and probably four of these five species belong to family Actinostolidae, one of the two richest families of deep-sea anemones (the other is Hormathiidae, to which *C. coronata* belongs).

We describe another member of Actinostolidae as a new genus and new species from the TAG (Trans-Atlantic Geotraverse) vent fields, located at 26°08.3′N, 44°49.6′W, and 3650 m. Part of the Mid-Atlantic Ridge (MAR), TAG is one of the largest submarine hydrothermal fields known (German et al. 1995, Van Dover 1998). We infer this to be the species Van Dover et al. (1997) reported preying on a shrimp of the species *Rimicaris exoculata* at the TAG site, and that is depicted in Fig. 3b of Van Dover (1995). Shrimp (along with fish and crabs) dominate high-temperature regions of the TAG vent field near active black smokers, and anemones occupy peripheral regions where the water is cooler (Van Dover 1995), attached to the crumbly substratum of oxidized sulfide.

Materials and methods.—The five specimens we studied were collected on 21 September 1994 using the claw of the submersible Mir 1. Within an hour of being brought to the surface, they were fixed in 10% seawater formalin; later they were transferred to isopropanol. Morphological aspects of this description are based on these preserved specimens; biological information is from the published literature and from P. A. Tyler, who provided the specimens to us. One well-expanded specimen, which we designated the holotype, was missing a few tentacles, but was otherwise in excellent condition. The four paratypic specimens were missing many tentacles and patches of ectoderm. Three of them were in good condition otherwise and were moderately expanded; the other was moderately contracted and its partly-everted actinopharynx was damaged.

Preparation of histological sections and the gathering of cnidae data followed methods of Fautin & Hessler (1989). Histological sections 8 μm thick were stained with hematoxylin and eosin. Cnidae were measured in smash preparations at 1000×.

Maractis, new genus

Definition.—*Maractis* has the following combination of diagnostic characters: member of family Actinostolidae having six pairs of complete mesenteries; mesenteries not arrayed according to the *Actinostola* rule; all mesenteries gametogenic; tentacles not thickened at the base; and no tentacular mastigophores. Further defining features include a broad base, at least 48 tapered tentacles, and column ectoderm that lacks papillae or other such structures. Animals of this genus are supple, unlike many deep-sea anemones, because the mesoglea is relatively thin.

Differential diagnosis.—In the key to some genera of Actinostolidae of Fautin & Hessler (1989), *Maractis* falls under options B), ff), hh), jjj), and kk) by virtue of having "All or all stronger mesenteries fertile . . . ," "Longitudinal tentacle muscles ectodermal," "No microbasic *b*-mastigophores in tentacles," "No tentacular mastigophores," and "Six pairs of mesenteries perfect," respectively.

Three genera fall under that option in the key: *Bathydactylus, Cnidanthea,* and *Epiparactis. Bathydactylus,* like *Maractis,* has a broad base. However, *Bathydactylus* has a very strong marginal sphincter muscle that forms a projecting wall, stout tentacles that are few in number, mesenteries that are not hexamerously arrayed, and papillae in the distal part of the column (at least in some species). *Cnidanthea,* like *Maractis,* has hexamerously arrayed mesenteries, but, unlike *Maractis,* has papillose nematocyst batteries on its column. *Epiparactis,* like *Maractis,* has more than 48 tentacles that are closely packed at the rim, and has broad pedal and oral discs. However, it has a smooth column and "thick, cartilaginous mesogloea" (Carlgren 1921, page 198).

The other genera of actinostolid sea anemones that have been reported from hydrothermal vents are *Marianactis, Parasicyonis,* and *Actinostola; Cyananthea* probably also belongs to this family. *Maractis* is similar to *Marianactis* Fautin & Hessler, 1989, in lacking microbasic *b*-mastigophores in the tentacles, but differs in lacking microbasic amastigophores in the tentacles. *Parasicyonis* Carlgren, 1921, and *Actinostola* Verrill, 1883, differ from *Maractis* both externally (both have short tentacles) and internally (in the former, mesenteries of only the last cycle are fertile, whereas in the latter those of the first two cycles are sterile). *Cyananthea* is incompletely known, but has twice as many mesenteries at the margin as at mid-column, in contrast to *Maractis.*

Etymology and gender.—*Maractis* is a composite of MAR (Mid-Atlantic Ridge) and "actis," Greek for ray or beam, a term often applied to anemones. Its gender is feminine.

Type species.—*Maractis rimicarivora,* new species.

Maractis rimicarivora, new species
Figs. 1–4

Description.—Pedal disc flat, margin scalloped because pulled inward at mesenterial insertions (Fig. 1), which are visible through disc. Diameter in animals examined 25–55 mm. Color in preservation same as that of column, oral disc, and tentacles—uniformly dull pink.

Column diameter 20–30 mm, length 10–

Fig. 1. *Maractis rimicarivora*: portion of holotype (KUNHM 01149). Note scalloped edge of pedal disc and long, longitudinally-furrowed tentacles. Raised circular spots are inferred to be artifacts—impressions of the perforations in a collecting device or storage container.

20 mm. P. A. Tyler (pers. comm.) remarked in life "the column looks very short" but was difficult to see because animals "always appear to have the [tentacle] crown [directed] to the camera."

Mesenterial insertions visible through body wall where ectoderm is missing. Ectoderm thin, eroded from many specimens. Surface texture rough: mesoglea and ectoderm thrown into short, relatively deep, complex folds (Figs. 2A, 3).

Oral disc torn or obscure in specimens examined. No fossa: outermost tentacles arise from margin (Fig. 2A). Tentacles 5–25 mm long (longest roughly equal to or slightly longer than column height). Flaccid, flattened in preserved specimens, longitudinally furrowed, tapering toward distal end (Fig. 1); number to nearly 100 in specimens examined. Cannot be withdrawn and covered when animal retracted. Longitudinal muscles ectodermal, continuous with radial muscles of oral disc (Fig. 2A).

Mesenteries regularly arrayed in 4 cycles, not according to the *Actinostola* rule; those of fourth cycle may not reach margin. Two pairs of directives, each attached to a siphonoglyph, lie diametrically opposite one another. Only mesenteries of first cycle complete. All fertile (including directives and those of highest order) (Fig. 3); sexes separate. No stomata. Retractor muscles well-developed, diffuse, arrayed in bolster-like strands (Fig. 3). Parietobasilar muscles developed only along stronger mesenteries; broad at base; each extends about half length of column, has very narrow free edge.

Marginal sphincter muscle mesogleal, moderately well developed. May fill entire width of mesoglea at margin but for most of length does not extend to ectodermal edge of mesoglea (Fig. 2B); at proximal end, occupies about half width of mesoglea, lying along endoderm (Fig. 2A, B). Small alveoli of equal size scattered along ectodermal side of sphincter; may be reticulate on endodermal side (Fig. 2A, B). Muscle cells relatively denser in larger individuals. Musculature weakly transversely stratified in parts of muscle of some individuals.

Actinopharynx about half length of column.

Animals, including tentacles, may remain fully extended upon preservation.

Cnidom.—spirocysts, basitrichs, microbasic *p*-mastigophores, holotrichs.

Size and distribution of cnidae.—Letters refer to illustrations in Fig. 4. Measurements in parentheses are of single capsules that fell outside the usual range. Number of capsules measured is indicated by "*n*"; ratio of the number of animals in which a particular type of cnida was found to the total number examined for that tissue is indicated by #.

Tentacles—distal end:		
Spirocysts (A, B) 30.0–78.5 × 2.8–7.3 (7.8) μm	*n* = 91	# = 5/5
Basitrichs (C) (15.6, 15.9) 17.2–25.5 × 1.6–2.9 μm	*n* = 54	# = 5/5
Basitrichs (D) 31.0–48.4 (54.6) × 2.5–3.8 μm	*n* = 50	# = 5/5
Holotrichs (E) 30.4–53.9 × 4.5–6.4 μm	*n* = 39	# = 5/5
Tentacles—proximal end:		
Spirocysts (A, B) 30.3–64.1 × 2.9–6.9 (7.7, 8.1) μm	*n* = 85	# = 5/5
Basitrichs (F) (16.8) 19.2–43.4 × 1.9–3.8 μm	*n* = 74	# = 5/5
Column:		
Basitrichs (F) 19.5–31.5 × 1.9–3.9 (4.9) μm	*n* = 71	# = 5/5
Microbasic *p*-mastigophores (G) 21.3–31.9 × 3.4–6.2 μm	*n* = 54	# = 4/5
Actinopharynx:		
Basitrichs (F) 23.4–34.9 × 2.3–3.2 μm	*n* = 9	# = 3/4
Microbasic *p*-mastigophores (G) 28.6–42.1 × 4.1–5.2 (5.7) μm	*n* = 31	# = 3/4
Mesenterial filaments:		
Basitrichs (C) 16.1–34.1 (39.3, 45.1) × 1.8–4.5 μm	*n* = 61	# = 5/5
Microbasic *p*-mastigophores (G) 26.9–38.9 (43.1) × 3.3–5.7 (6.0) μm	*n* = 61	# = 5/5

Most spirocysts could be assigned to one of two types (both shown in Fig. 4A), although rare ones shared characteristics of both. This distinction was not noticed until many measurements had been gathered, so our data are not divided by type. Spirocysts that were, on average, longer and wider had tubules wound in an untidy fashion and lacked space between the tubule and the capsule's posterior end (Fig. 4A, at left). Spirocysts that were, on average, shorter and narrower had neatly wound tubules and space between the tubule and the posterior end of the capsule (Fig. 4A, at right, and Fig. 4B). For example, in tentacles of paratype KUNHM 01150, 9 of the "neat" spirocysts measured 36.0–49.9 × 3.3–5.3 μm, and 10 of the "untidy" ones measured 37.3–59.2 × 5.1–7.7 μm.

Etymology.—The name *rimicarivora* refers to the ingestion (Latin vora: to eat) by this anemone of the shrimp *Rimicaris exoculata* Williams & Rona, 1986. [The taxonomy of vent shrimps is considered by Shank et al. (1998).]

Type locality.—TAG (Trans-Atlantic Geotraverse) hydrothermal vent fields: 26°08.3′N, 44°49.6′W; 3650 m.

Type specimens.—Holotype (Fig. 1) Division of Invertebrate Zoology, University of Kansas Natural History Museum (KUNHM) 01149: a dissected male specimen and 16 microscope slides made from it.

Paratypes: KUNHM 01150: a dissected specimen of indeterminate sex and 20 microscope slides made from it. The Natural History Museum, London 1999.80: a dissected male specimen and 9 microscope slides made from it. The Santa Barbara Museum of Natural History, Santa Barbara, California 145140: a dissected female specimen and 10 microscope slides made from it. The U.S. National Museum of Natural History 100132: a dissected specimen of in-

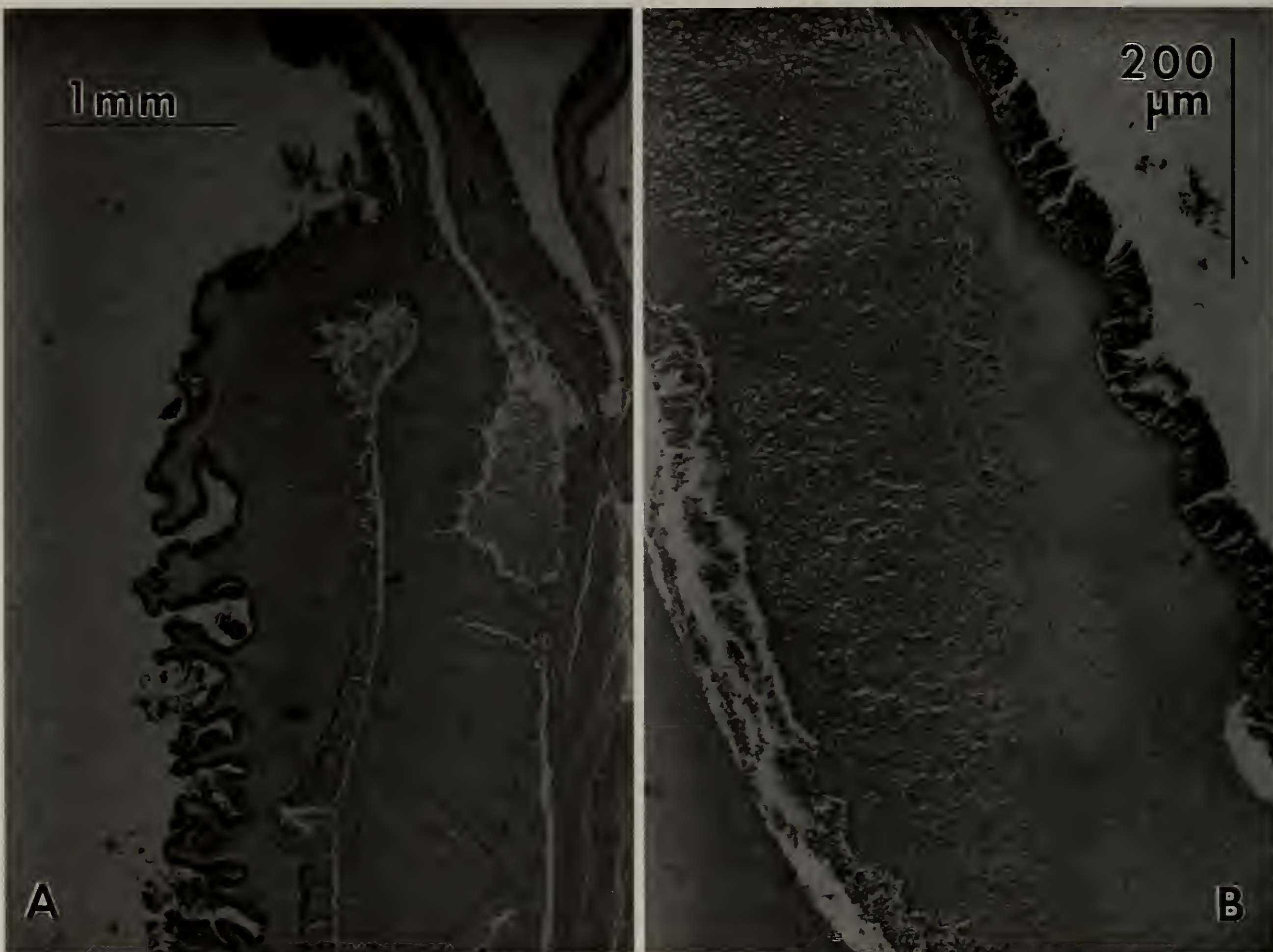

Fig. 2. Mesogleal sphincter muscle of *Maractis rimicarivora*. A: Longitudinal section at margin of paratype KUNHM 01150. Tentacles have ectodermal longitudinal musculature; outermost tentacle arises at margin. The surface of the animal is thrown into short, complex folds. B: Proximal end of sphincter muscle of holotype (KUNHM 01149).

determinate sex and 5 microscope slides made from it.

Discussion

The holotype (KUNHM 01149), a quarter of which is illustrated in Fig. 1, has conspicuous raised circular patches on part of its column, especially the lower portion. We initially thought these might be adhesive structures to which sulfide particles could adhere (see below). We concluded, however, that they are artifacts from a collecting device or storage container. Their position does not correspond to any anatomical feature of the animal, they are on only one side of the holotype, and they are not visible in the other specimens (although the ectoderm is eroded from several of them, patches persist).

We, like Van Dover et al. (1997), found no evidence of bacterial symbionts in *Maractis rimicarivora*: there were neither bodies that could be interpreted as bacteria nor structures of the animal that were likely to harbor bacteria. In addition, Van Dover et al. (1997) found no biochemical or physiological evidence of bacterial symbiosis. We infer, therefore, that *M. rimicarivora* is a typical cnidarian in depending on prey for energy and nutrients. Shrimp and anemones dominate the biota of TAG and most other Atlantic vent fields that have been studied, in contrast to Pacific vent fields, which are dominated by tubeworms, mussels, and clams (Van Dover 1995). At TAG, there appears to be little aside from shrimp on which the anemones could feed (P. A. Tyler, pers. comm.). The observation of predation

Fig. 3. Cross-section at mid-column level of the holotype (KUNHM 01149). Spermaries associated with mesenteries of the third and fourth (highest) orders are visible. Well-developed retractor muscles are diffuse. Scale bar = 1 mm.

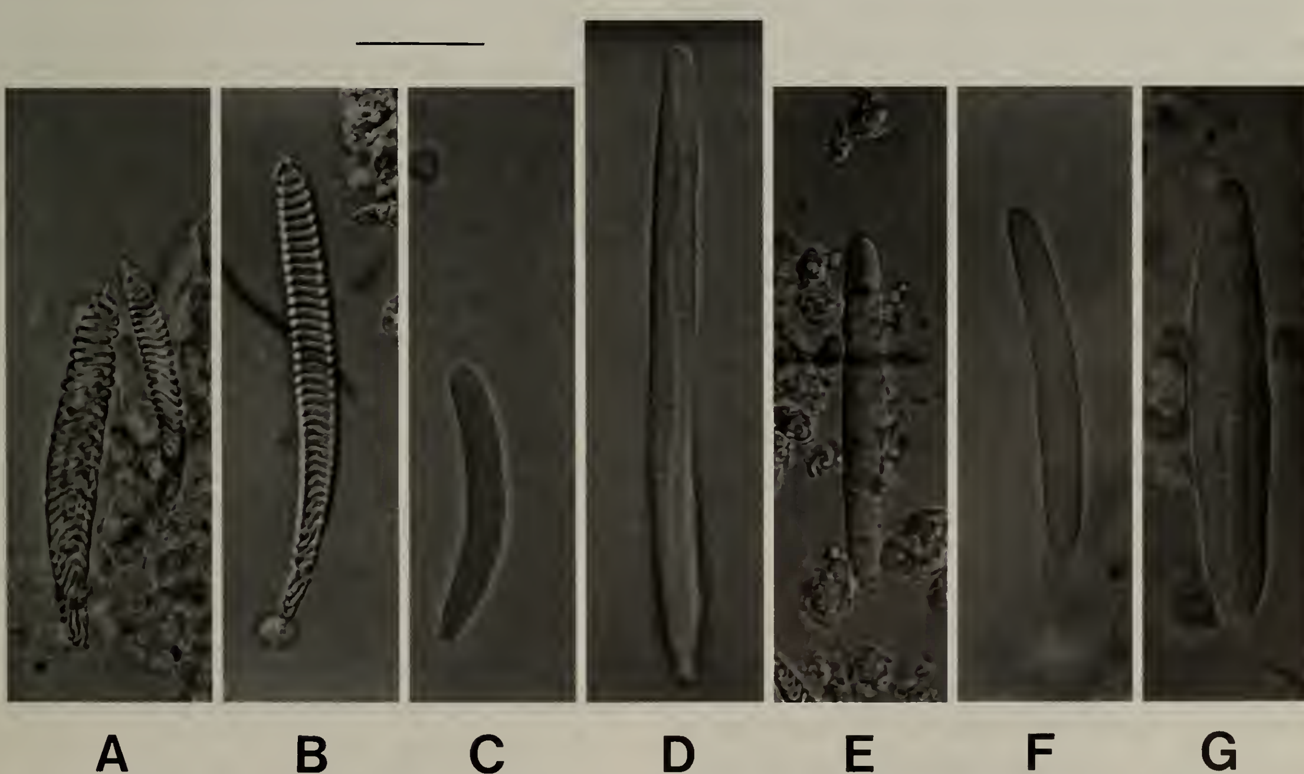

Fig. 4. Cnidae of *Maractis rimicarivora*. See text for explanation. Scale bar = 9 μm.

on a shrimp (Van Dover et al. 1997) is consistent with these data and inferences.

The size and color of the predatory anemone, and the length of its tentacles, were consistent with our specimens. However, our specimens lacked the black spots on the column that are conspicuous in the videotape on which the report of Van Dover et al. (1997) is based. Van Dover (pers. comm.) suggested they were sulfide particles. Although the specimens we studied lacked discrete adhesive structures, the large surface area of their wrinkled ectoderm (Figs. 2, 3) would seem likely to have adhesive properties. Indeed, some fine debris adhered to one specimen we studied. We therefore concluded the animal that is the subject of the report by Van Dover et al. (1997) is *M. rimicarivora.* Van Dover et al. (1997) found the anemone most abundantly 30–40 m from the center of a black smoker, where its density reached nearly 200 m^{-2}; its average density in the ring it formed around the black smoker at a distance of about 15–60 m was 3 m^{-2}, so the anemones probably do not experience water of elevated temperature.

Van Dover (1995) inferred there might be two species of anemones at TAG, one small and one large. One small anemone specimen we examined had a short, strongly reticulate mesogleal sphincter muscle, which was like that of neither *M. rimicarivora* nor *Paractinostola ingolfi,* the anemone collected at the Snake Pit hydrothermal vent field 3° south of TAG (Segonzac 1992). Therefore, there may be at least three species of anemones at TAG. Anemones also occur at the Broken Spur vent field 3° north of TAG (Van Dover 1995), but not at the Lucky Strike vent field 11° north of TAG (Van Dover et al. 1996).

Acknowledgments

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